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Abstract

Paleoecological reconstructions using lake sediments provide important information about ecological dynamics and forest disturbance processes that occurred prior to the historic period of scientific observation. In high-altitude and high-latitude ecosystems where landscape-scale disturbances recur at time intervals exceeding observation in many regions, e.g. western North America, reconstructed environmental data are essential in providing context for land managers. During the most recent two decades eruptive populations of bark beetles (*Dendroctonus* spp.) have rapidly and profoundly altered subalpine forest ecosystems across western North America. Outbreaks of these insects are unprecedented in scale and severity, at least historically. Currently, little information exists about these destructive outbreaks and in general, the information that exists, does not extend beyond the most recent few centuries. The research presented here examines sedimentary pollen records from six subalpine basins affected by severe spruce beetle (*D. rufipennis*) epidemics during the 20th century in the high-elevation plateaus and mountain ranges of south-central Utah. Reciprocal exchanges in dominance between pollen abundance of host spruce (*Picea engelmannii*) and non-host subalpine fir (*Abies lasiocarpa*) associated with historic outbreaks are conspicuous. Calculating simple ratios of host and non-host pollen accumulations offers a useful metric to visually identify spruce beetle outbreaks using sedimentary records. However, supporting lines of evidence may be required to identify these disturbances with greater certainty over the Holocene. Our data and findings provide a platform with which to begin exploration of other paleoecological proxy methods for the ultimate purpose of generating more temporally extensive reconstructions of bark beetle disturbances using sedimentary records.

Keywords

Abies lasiocarpa, *Dendroctonus*, disturbance, *Picea engelmannii*, pollen, sediment, spruce beetle, subalpine forests

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Introduction

Pollen and charcoal preserved in lake sediments are critical indicators for reconstructing the influence of past climates and vegetative conditions on landscape disturbance. Sedimentary charcoal provides valuable information about wildfire variability across local, regional, and global scales (Higuera et al., 2007; Long et al., 1998; Power et al., 2009; Whitlock and Millspaugh, 1996). Sedimentary pollen and macrofossils can be used to infer non-fire disturbances such as phytophagus insect epidemics and fungal blights (Anderson et al., 1986; Brunelle et al., 2008; Davis, 1981; Morris et al., 2010). For example, sedimentary pollen records enabled the reconstruction of a mid-Holocene outbreak of two defoliators in eastern North America; the spruce budworm (*Choristoneura fumiferana*) and hemlock looper (*Lambdina fiscelaria*) (Allison et al., 1986; Fuller, 1998; Shuman et al., 2005). Similarly, the decline of American chestnut (*Castanea dentata*) beginning in 1904 CE from the introduction of a non-native pathogen (chestnut blight; *Endothia parasitica*) is also well-documented in sedimentary sequences (Anderson, 1974; Brugam, 1978; Davis, 1981). In Europe, declines of elm pollen (*Ulmus* spp.) during the mid-Holocene are attributed to infection from a fungal pathogen (*Ophiostoma ulmi*) and possibly an epidemic of elm bark beetle (*Scolytus scolytus*) concomitant with widespread forest clearance for agriculture (Fossitt, 1994; Innes et al., 2003; Rasmussen, 2005; Watts, 1961).

Spruce beetle (SB; *Dendroctonus rufipennis*) and mountain pine beetle (MPB; *D. ponderosae*) account for the most significant numbers of tree mortality in higher elevation forests in western North America (Fettig et al., 2007; Raffa et al., 2008) and damage from these insects equals (Baker and Veblen, 1990) or exceeds (Logan and Powell, 2001) the ecological and economic impacts of wildfire in this region. It is therefore surprising that only recently have paleoecological studies sought to reconstruct these disturbances using lake sediments (Anderson et al., 2010; Brunelle et al., 2008; Morris et al., 2010).

Dendroecological records from Colorado and Utah suggest that SB outbreaks recur at *c*. 120 yr intervals based on multicentury data sets (DeRose and Long, 2007; Veblen et al., 1994) while records from Alaska indicate 48 yr intervals (Sherriff et al., 2011). These records essentially encompass two climatic periods: (1) the cool and dry 'Little Ice Age' (Bradley and Jones, 1993; Crowley and Lowery, 2000; Petersen, 1994) and (2) the 19th and 20th

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centuries. The last century in particular is characterized by anthropogenic climate warming (e.g. Mann et al., 1999) as well as land-use changes in subalpine forests from logging (Baker, 1992) and fire suppression (Romme and Despain, 1989). A significant amount of research suggests that eruptions of bark beetle populations in the last two decades may be unprecedented in scale and severity because of interacting mechanisms of climate warming, prolonged drought, and increased stand density (Bentz et al., 2010; Breshears et al., 2005; Hicke et al., 2006; Logan and Powell, 2001; Raffa et al., 2008).

Furthermore, recent research using tree rings suggests that climate teleconnections, specifically the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997) and El Niño-Southern Oscillation (ENSO) (Diaz and Markgraf, 2000), influence the recurrence of bark beetle populations (Macias-Fauria and Johnson, 2009; Sherriff et al., 2011). Persistent states of ENSO and PDO have occurred over the Holocene (Clement et al., 2000; Koutavas et al., 2002; Moy et al., 2002) due to differences in received solar radiation relative to modern (Berger and Loutre, 1991; Kutzbach et al., 1998). These conditions created moisture and temperature regimes during the early and middle Holocene not wholly analogous to the range of conditions experienced during the last several centuries in western North America recorded by tree ring records in this region (e.g. Veblen et al., 1994). However, understanding ecological and disturbance conditions during the early and middle Holocene are useful in anticipating changes during future warming scenarios for the 21st century (Meehl et al., 2007). Furthermore, the absence of a method for reconstructing bark beetle disturbances over the Holocene indicates that the current understanding of these disturbances and potential relationships with wildfire are based on a limited assessment of climate conditions.

Davis (1981) provides the foundation for using sedimentary pollen to reconstruct non-fire ecological disturbances. Upon examination of numerous Holocene pollen sequences, Davis (1981) noted acute declines in the influx and percentage of eastern hemlock which she described as 'virtually instantaneous' (Davis, 1981). Fuller (1998) reiterates the magnitude and rapidity of hemlock pollen reductions noted by Davis and subsequent work identified similar outbreak signals in at least 60 pollen records (Bennett and Fuller, 2002). Both Davis and Fuller also observed increases in pollen accumulation of competitive arboreal species (birch (*Betula*), beech (*Fagus*), and oak (*Quercus*)) concurrent with the hemlock decline. Davis (1981) reasoned that this disturbance event was triggered by an organism because (1) no sedimentary charcoal was found coincident with the hemlock decline that would suggest wildfire mortality; (2) climate would influence at least several species simultaneously, not simply hemlock alone; and (3) the coherency of the pollen decline is synchronous across a broad geographic region suggesting eruptive populations of an organism. Owing to the presumably sparse population densities of humans in eastern North America during the middle Holocene (Russell, 1983; Vale, 2002), it appears unlikely that a systematic selection by humans of hemlock for fuel or construction purposes occurred, particularly across a broad geographical region (Allison et al., 1986; Davis, 1981). An insect outbreak was later confirmed by secondary physical evidence in lake sediments (Anderson et al., 1986) including lepidopteron remains that co-occurred stratigraphically with declines of hemlock pollen.

The mid-Holocene hemlock decline is an important example of detecting and interpreting ecologically significant non-fire disturbances and strengthens the validity of using pollen to reconstruct bark beetle outbreaks. However, two significant differences exist among the mid-Holocene hemlock decline and modern bark beetle outbreaks. First, the hemlock decline is suggested to be caused by the arrival of an organism to a naïve host, perhaps similar to the American chestnut blight (Allison et al., 1986; Calcote, 2003; Davis, 1981), whereas bark beetles are native insects and their presence is documented in subalpine forests in western North America at least over the Holocene (Brunelle et al., 2008) and probably much longer (Maroja et al., 2007). Second, the hemlock decline is conspicuous in pollen records because the decreased abundance of hemlock pollen was sustained over several centuries. This circumstance is due in part to middle-Holocene climate conditions, specifically decreases in January temperature and precipitation which were unfavorable for hemlock. Colder and drier winters probably decreased host vigor (hemlock) and limited re-establishment opportunities for hemlock (Calcote, 2003). In contrast, bark beetle outbreaks are generally not known to trigger sustained suppression of their hosts trees and are discrete events when compared with the hemlock decline. Bark beetle disturbances persist in epidemic (outbreak) population phase for at most only a few decades. Therefore sediment compression and sampling resolution are considerable limitations in reconstructing relatively short bark beetle disturbances, despite significant tree mortality, when compared with the middle-Holocene hemlock decline. Third, the unreliability and poorly understood taphonomy of bark beetle remains is problematic (Morris, 2008; Watt, 2008) particularly in the absence of other secondary evidence (e.g. geochemical markers). Despite dramatic and virtually instantaneous pollen declines, it remains speculative to assume that bark beetles are responsible because other outbreaks of other phytophagus insects (or pathogens) could conceivably have occurred, e.g. western spruce budworm (*Choristoneura occidentalis*).

However, understanding the pollen signature of a bark beetle outbreak is an important and critical first step in determining a methodology and/or suite of analyses for reconstructing these disturbances. Existing studies that examine sedimentary pollen from SB-affected landscapes demonstrate spruce pollen declines while fir pollen increases in response to the insect outbreak (Anderson et al., 2010; Morris et al., 2010). This reciprocal relationship between spruce and fir pollen mirrors host/non-host stand conditions reported during SB epidemics including ground surveys (Dymerski et al., 2001), stand age reconstructions (DeRose and Long, 2007), and growth patterns observed in tree rings (Veblen et al., 1994). Vegetation surveys suggest that other understory components, including shrubs and herbs, are also more successful (such as fir) following the loss of canopy-dominant spruce (Kulakowski et al., 2003; Kulakowski and Veblen, 2006; Schmid and Hinds, 1974; Veblen et al., 1994). The purpose of this study is to broaden the single-basin approach of Anderson et al. (2010) and Morris et al. (2010) by examining pollen accumulation in lake sediments from multiple replicate sites within watersheds affected by severe SB outbreaks during the 20th century to determine whether the palynological response is robust on the landscape-scale to known SB disturbance.

Study area

The Colorado Plateau is punctuated at its western margin in central and southwestern Utah by a series of subalpine plateaus that traverse the eastern Great Basin (Wannamaker et al., 2001). These plateaus rise steeply from the surrounding desert valleys and the

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towering relief of these landforms facilitates orographic precipitation gradients where moisture receipt is controlled by elevation, with greater amounts of precipitation received at higher elevations. In the subalpine zone (2700 m to 3400 m), most moisture is received as snowfall during winter and spring months with a secondary peak in precipitation during late summer from convective storms. The study area lies on the transition zone of summer-dominant (monsoon) and winter-dominant (Pacific) moisture regimes (Mitchell, 1976; Mock, 1996) and south of the 42°N ENSO dipole boundary (Wise, 2010), resulting in variable seasonal and annual precipitation accumulation (Cayan, 1996; Hidalgo and Dracup, 2003; Mock, 1996; Shinker, 2010). The forests on the summits of these plateaus are composed of Engelmann spruce/subalpine fir (*Picea engelmannii*/*Abies lasiocarpa*). Unlike subalpine ecosystems at comparable elevations in Colorado and northern Utah, lodgepole pine (*Pinus contorta*) is absent in south-central Utah.

Wasatch Plateau

The Wasatch Plateau (WP) is oriented north–south and covers an area of 2477 km^2. Elevations average 3350 m across the summit of the plateau. The WP is capped by limestone, causing surface water to be moderately alkaline (9+) in pH (Morris et al., 2010). The WP was glaciated during the Pleistocene by alpine-style glaciers which created numerous cirques and deposited moraine and till features that are particularly conspicuous on north-facing aspects (Osborn and Bevis, 2001). Land-use changes following settlement by Euro-Americans at *c*. 1850 CE included lumber harvesting and livestock grazing (cattle, sheep) in subalpine meadows (Ellison, 1954; Hall, 2001). Many of these meadows were so severely denuded of vegetation that erosion removed the A soil horizon, increasing drought susceptibility (Gill, 2007; Klemmedson and Tiedemann, 1998).

A landslide in 1984 CE facilitated establishment of SB populations in downed spruce (Hebertson and Jenkins, 2007). A landscape composed of susceptible hosts, coupled with warm and dry conditions during the 1990s CE, were favorable for the development of a SB epidemic that killed >95% of mature Engelmann spruce (Dymerski et al., 2001). Blue Lake (39°3'20.33"N, 111°30'17.43"W) and Emerald Lake (39°4'26.72"N, 111°29'50.964"W) (Figure 1, Table 1) occupy north-facing cirque basins. Elevation and lake size for Blue and Emerald lakes are 3129 m and 3.2 ha, and 3090 m and 3.3 ha, respectively. Both lakes are surrounded by dead Engelmann spruce from the 1980–1990s CE SB outbreak (Figure 1, panel b). Residual subalpine fir are present in both watersheds. Limber pine (*Pinus flexilis*) is occasionally present at rocky, exposed locales and isolated blue spruce (*Picea pungens*), a less preferred host for SB, can be found in particularly mesic sites. Aspen (*Populus tremuloides*) are currently absent in both basins but are found at similar elevations on the WP.

Aquarius Plateau

The Aquarius Plateau (AqP) is the highest elevation landform in the study area with a mean elevation of 3355 m, covering an area of 2330 km^2. The summit of the AqP exhibits rolling tabletop topography and is composed of andesitic basalt that originated during the Oligocene Marysvale Volcanic episode (Flint and Denny, 1958). The AqP was occupied by a ≈200 m thick ice cap during the Pleistocene (Flint and Denny, 1958; Osborn and Bevis, 2001) and glacigenic features on the AqP are generally erosional that include roche moutonnées, thin soils, and glacial abrasions (striations, chatter marks) (Marchetti et al., 2005). The AqP is dominated by spruce-fir forests with the highest elevations consisting of pure Engelmann spruce stands with interspersed grasslands (Schmid and Hinds, 1974). Other arboreal species include subalpine fir, limber pine, aspen, blue spruce, and bristlecone pine (*Pinus longaeva*).

A SB epidemic beginning around 1916–1918 CE persisted into the 1930s CE killed >80% of mature Engelmann spruce (Dixon, 1935; Mielke, 1950). Banana Lake (38°4'0.29"N, 111°35'12.21"W) and Purple Lake (38°4'28.33"N, 111°34'16.47"W) (Figure 1, Table 1) are kettle lakes occurring at 3128 m and 3226 m, respectively. Lake size for Banana and Purple lakes are 10.6 ha and 6.2 ha, respectively. Both basins are surrounded by dense stands of Engelmann spruce, subalpine fir, and blue spruce with occasional aspen patches. Subalpine fir is rare at Purple Lake when compared with the other watersheds discussed here. Snags from the 1920s CE SB outbreak are visible in both watersheds (Figure 1, panels b and c).

Markagunt Plateau

The Markagunt Plateau (MP) trends north–south and covers an area of 2100 km^2 with an average elevation of 3320 m. Holocene-age lava flows dating to ≈1200 years ago overlay limestone creating a vulcano-karst landscape that drains rapidly, increasing drought susceptibility (Wilson and Thomas, 1964). A thin ice sheet occupied the top of the MP during the Pleistocene and occasional examples of depositional features are present, including recessional moraines and glacial till (Osborn and Bevis, 2001).

The MP experienced a severe SB outbreak beginning in the 1990s CE with eruptive SB populations building in remnant logging debris and windthrow that eventually killed >93% of Engelmann spruce across all class sizes (DeRose and Long, 2007). Alpine Pond (37°38'11.22"N, 112°49'26.75"W) and Morris Pond (37°40'25.48"N, 112°46'49.75"W) (Figure 1, Table 1) have elevations of 3172 m and 3125 m and lake size of 0.1 ha and 0.7 ha, respectively. Alpine Pond and Lowder Creek Bog were cored in paleoecological studies conducted prior to the SB outbreak (Anderson et al., 1999; Mulvey et al., 1984). Morris Pond is a moraine-dammed lake located 1.5 km north of Lowder Creek Bog. Alpine and Morris Ponds are surrounded by ghost forests of dead Engelmann spruce, with abundant residual subalpine fir and occasional aspen and limber pine (Figure 1, panel b). Bristlecone pine occurs in the Alpine Pond watershed.

Methods

Site selection

Characteristics of lakes selected for this study included USDA Forest Service documentation of a severe 20th century SB outbreak (Hebertson and Jenkins, 2008), the presence of spruce-fir forest with visually detectable SB-caused mortality, limited inflow/outflow of surface water, unmodified by significant man-made impoundments, absence of stand-replacing wildfire during the 20th century, and no evidence of large-scale salvage logging to remove beetle-killed trees. Based on these criteria, six basins were selected and cored using modified piston devices between 2005 and 2009. Information regarding bark beetle outbreaks is inherently qualitative, even during the historical period. Unlike fire, modern detection of the onset and collapse of bark beetle eruptions are often difficult to assess (Hebertson and Jenkins,

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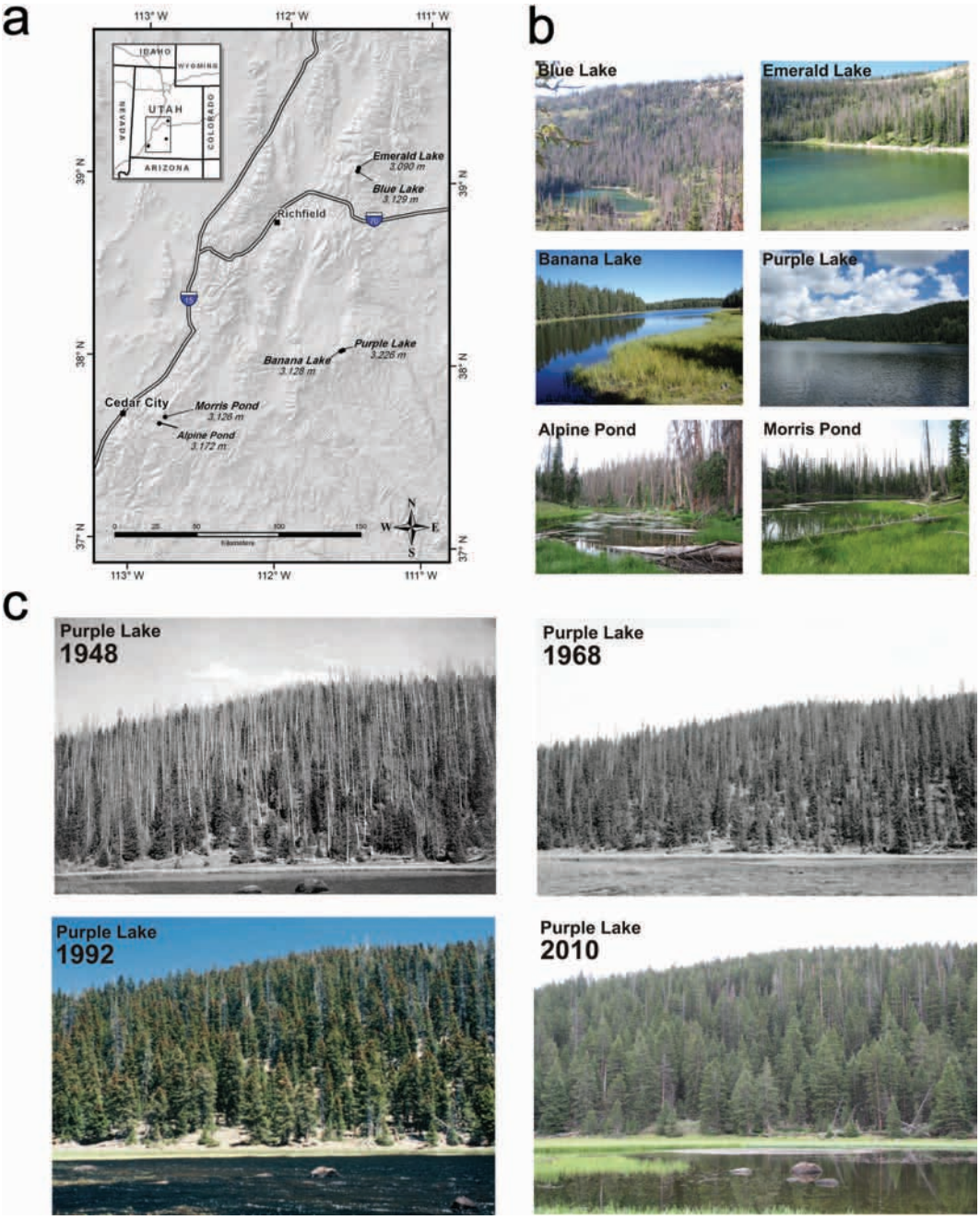

Figure 1. (a) Location map of central and southern Utah showing the locality of the six basins in the study area. (b) Photographs taken during field work of basins selected for this study which are Blue and Emerald lakes (looking south) located on the Wasatch Plateau, Banana and Purple lakes (looking west) located on the Aquarius Plateau, and Alpine and Morris ponds (looking west and east, respectively) located on the Markagunt Plateau. (c) Repeat photographs of Purple Lake taken from the same photopoint looking north (note location of rocks in foreground). These images depict the mortality of Engelmann spruce (*Picea engelmannii*) following the 1930s spruce beetle (*Dendroctonus rufipennis*) outbreak and forest regeneration in subsequent decades. Photographs of Purple Lake from 1948 in Mielke (1950), 1968 and 1992 provided by A Steve Munson (USDA Forest Service). All other photographs taken by Jesse Morris.

Table 1. Summary of location, elevation, and lake size data for basins analyzed in this study.

Coring Site	Landform	Designation	Coordinates		Elevation (m)	Lake Size (ha)
Blue Lake	Wasatch Plateau	Manti-LaSal NF[a]	39° 3' 20" N	111° 30' 17" W	3129	3.2
Emerald Lake	Wasatch Plateau	Manti-LaSal NF	39° 4' 26" N	111° 29' 50" W	3090	3.3
Banana Lake	Aquarius Plateau	Dixie NF	38° 4' 30" N	111° 35' 12" W	3128	10.6
Purple Lake	Aquarius Plateau	Dixie NF	38° 4' 28" N	111° 34' 16" W	3226	6.2
Alpine Pond	Markagunt Plateau	Cedar Breaks NM[b]	37° 38' 11" N	112° 49' 26" W	3172	0.1
Morris Pond	Markagunt Plateau	Dixie NF	37° 40' 25" N	112° 46' 49" W	3126	0.7

[a]National Forest under stewardship of the US Department of Agriculture National Forest Service.
[b]National Monument under stewardship of the US Department of the Intererior National Park Service.

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2008). Insect disturbances on public lands are detected, observed, and mapped from fixed-wing aircraft to generate aerial sketch-maps of defoliation and mortality, which are subjective according to each individual observer (McConnell, 1999).

Chronology

Chronology for the six cores discussed here was achieved using ^{210}Pb and ^{137}Cs analysis (Figure 2; Table 2). The upper 24 cm of each sediment core was subsampled (5 cc) and 2 cm interval was homogenized (e.g. 2–4 cm) yielding 12 subsamples for each core, with the exception of Blue Lake, which was sampled a 1 cm interval for the first 20 cm (Morris et al., 2010). Subsamples were weighed and dried in a muffle furnace at 100°C to remove water. Dehydrated samples were submitted to Dr James Budahn at the US Geological Survey Laboratory in Denver, CO for analysis. The ^{210}Pb profile was interpreted by Dr Budahn using Appleby's Constant Rate of Supply Model (Appleby et al., 1979). When possible, the 1963 CE peak in ^{137}Cs associated with the climax of atmospheric detonation of nuclear test weapons was used to constrain the ^{210}Pb chronology. Core-top samples were assigned to the year of core collection (Table 2). Final age–depth assignments were generated by Dr Budahn. Though the dated sediment records extend to the 19th century, only data from the 20th century to the year of coring are presented.

Pollen analysis

Pollen samples (1 cc) were processed at 1 cm intervals for the upper 24 cm for each core. Each sample was processed to isolate pollen following methods established by Faegri et al. (1989). *Lycopodium*, an exotic spore, was introduced to each sample during processing as a tracer. Slide-mounted pollen samples were examined using light microscopy at 500× and counted to a minimum of 300 terrestrial grains. Identification of grains was aided by laboratory reference collections and relevant dichotomous keys and literature (Bassett et al., 1978; Erdtman, 1952; Kapp et al., 2000).

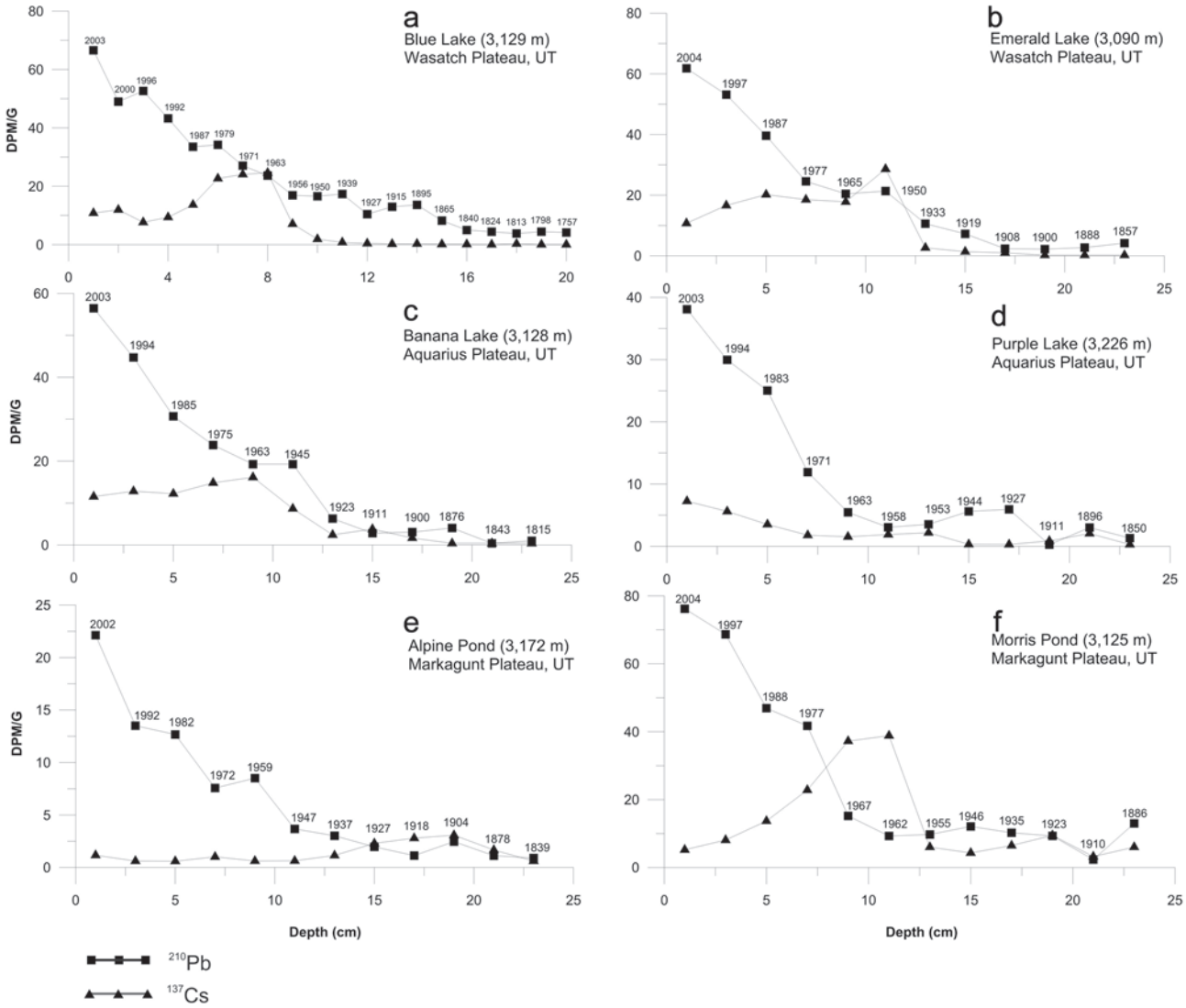

Figure 2. Plots for unsupported ^{210}Pb (black line, black squares) and ^{137}Cs (gray line, black triangles) data in DPM/G for the six historic sediment cores discussed in this manuscript. 5 cc sediment samples from homogenized 2 cm increments (1 cm for Blue Lake) were prepared in the RED Lab at the University of Utah in Salt Lake City. Dehydrated samples were submitted for analysis to Dr James Budahn at the USGS in Denver, CO. Dates for ^{210}Pb were assigned by the analytical laboratory using Constant Rate of Supply Model (Appleby et al., 1979) and assigning a peak in the ^{137}Cs profile (when observed) to the year 1963 CE.

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Table 2. Summary of age–depth relationships for historic sediments.

	Wasatch Plateau					Aquarius Plateau				Markagunt Plateau			
Depth (cm)[ab]	Blue Lake (Year CE)[c]	+/-	Depth (cm)[ab]	Emerald Lake (Year CE)[c]	+/-	Banana Lake (Year CE)[c]	+/-	Purple Lake (Year CE)[c]	+/-	Alpine Pond (Year CE)[c]	+/-	Morris Pond (Year CE)[c]	+/-
0	2005	0	0	2007	0	2007	0	2007	0	2007	0	2008	0
1	2003	1	2	2004	2	2003	2	2003	4	2002	5	2003	2
2	2000	1	4	1997	2	1994	3	1994	5	1992	6	1993	2
3	1996	1	6	1987	2	1985	3	1983	6	1982	7	1983	3
4	1992	1	8	1977	3	1975	4	1971	7	1972	9	1973	3
5	1987	2	10	1965	4	1963	5	1963	9	1959	11	1967	4
6	1979	3	12	1950	5	1945	7	1958	9	1947	14	1964	5
7	1971	4	14	1933	7	1923	10	1953	9	1937	15	1960	6
8	1963	4	16	1919	9	1911	12	1944	10	1927	17	1956	9
9	1956	5	18	1908	9	1899	13	1927	12	1918	17	1953	10
10	1950	6	20	1900	9	1876	18	1911	14	1904	19	1950	11
11	1939	7	22	1888	8	1843	26	1896	14	1878	23	1948	12
12	1927	8	24	1857	7	1815	22	1851	18	1839	24	1884	15
13	1915	9											
14	1895	12											
15	1865	16											
16	1840	22											
17	1824	26											
18	1813	26											
19	1798	25											
20	1757	27											

[a]Depth below mud-water interface, upper-most sample assigned to year core was collected.
[b]Bulk sediment samples (5 cc) submitted to James Budahn at US Geologic Survey in Denver, Colorado.
[c]Age-depth assignments provided James Budahn using ^{210}Pb Constant Rate of Supply Model (Appleby *et al.* 1979) and ^{137}Cs peak.

Though numerous pollen types were identified and counted, the pollen data presented here are generally grouped to family level and focus on subalpine groups that are most likely to respond to Engelmann spruce mortality. Shrub and herb pollen are combined into non-arboreal pollen (NAP). Pollen records are described in terms of percent, influx, and ratios. Pollen percent provides information about relative vegetation composition (inter-relatedness of taxa), influx provides information about individual taxa abundance, and ratios allow for consideration of single taxon versus a group of taxa, or another single taxon. Pollen ratios were calculated using the formula $(a-b)/(a+b)$ (Maher, 1963, 1972) which is useful in assessing ecological change from both climate and disturbance (Mensing et al., 2008). In all instances a represents spruce pollen and b represents various combinations of arboreal and non-arboreal pollen. Ratio data are presented in standard units (SU). Higher (lower) ratio values reflect greater (lesser) abundance of spruce pollen relative to other taxa.

Macrofossil analysis

Samples for charcoal and macrofossil analysis (5–10 cc) were collected and analyzed for the upper 24 cm of each core and were prepared following methodologies discussed by Whitlock and Millspaugh (1996). Sediment samples were screened using 125 µm and 250 µm nested sieves. Retrieved materials were placed on gridded petri dishes and then examined and counted using light microscopy at 40×. Because sites selected for this study intentionally excluded watersheds with evidence (or record) of high severity and/or spatially large fires, charcoal accumulations were virtually non-existent and when charcoal did occur, it was at very low concentration (<3 pieces/cm^3). Therefore charcoal data are not reported. Insect macrofossils meeting general criteria of bark beetles (*Dendroctonus* spp., *Ips* spp.) were submitted to Dr James Pitts at Utah State University in Logan, UT for identification.

Results

Wasatch Plateau

The Wasatch Plateau pollen assemblages (Blue and Emerald lakes) have similar arboreal components throughout the 1900s CE, featuring abundant spruce (20–30%) and pine (20–25%) pollen, with fir (10%) and aspen (≤5%) also at both sites (Figures 3 and 4). Conifer pollen influx is greater at Emerald Lake (e.g. spruce averages 4000 grains/cm^3 versus 800 grains/cm^3 at Blue Lake) (Figure 4). The shrub community at both lakes is dominated by sagebrush (*Artemisia*) (20–23%) with rose family (Rosaceae) (3–4%) and buckbrush family (Rhamnaceae) also present (1–2%). Shrub pollen influx averages are similar between both sites for sagebrush (1500 grains/cm^3), rose (950 grains/cm^3), and buckbrush (150 grains/cm^3). Herbaceous taxa are dominated by grasses (Poaceae) (9–10%) and members of the sunflower family (Asteraceae) (3–4%) with influx averages of 750 and 2000 grains/cm^3 for Blue and Emerald, respectively. Other herbaceous components are present at low values (e.g. 1–2%; <100 grains/cm^3) including smartweed (Polygonaceae), buttercup (Ranunculaceae), and bean families (Fabaceae). The ratio assemblage at both lakes displays similar trends where spruce pollen is reduced relative to other taxa early in the 20th century (*c.* 1910 CE), becomes dominant through the mid-century, and declines again before *c.* 1990 CE (Figures 3 and 4).

Aquarius Plateau

The arboreal Aquarius Plateau assemblages are dominated by spruce (30–40%) and pine (15–20%) with fir pollen more abundant at Banana Lake (8%) than at Purple Lake (<3%) (Figures 5 and 6). Aspen pollen is greater at Purple (20%) than at Banana Lake (7%). Pollen influx of all tree species except fir is higher at Purple Lake (Figure 6). Shrub pollen at both lakes are composed largely of rose (5%) and sagebrush (12%) while influx for both taxa is relatively higher at Purple Lake than at Banana Lake.

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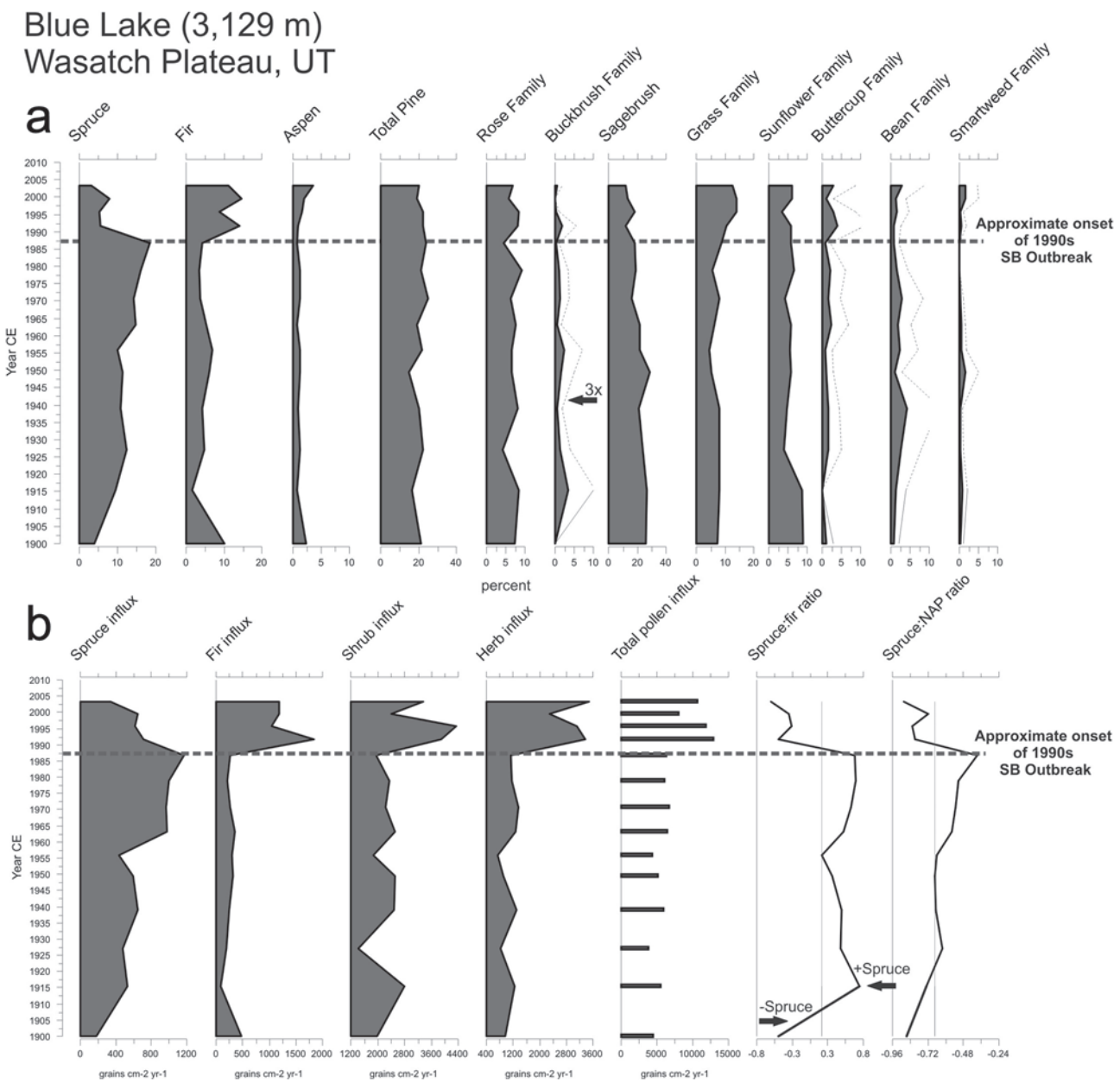

Figure 3. 20th century pollen percent (a) and pollen influx and ratio (b) plots for Blue Lake, located on the Wasatch Plateau, UT. Dashed plot lines indicate 3× exaggeration. A severe spruce beetle outbreak impacted the subalpine forests surrounding Blue Lake beginning in the late 1980s CE. Pollen ratios were calculated using $(a-b)/(a+b)$ where a represents spruce (host) and b represents fir and non-arboreal pollen (NAP; non-host). Higher ratio values indicate greater abundance of spruce pollen whereas lower values indicate less spruce pollen. Ratio thresholds are calculated as the 20th century ratio average (gray line).

Herbaceous taxa are dominated by grasses (4–5%) and members of the sunflower family (3–4%) and influx averages are greater at Banana Lake than at Purple Lake. Other herbaceous components are present at low values (1–2%; <100 grains/cm^3) including mustards (Brassicaceae), smartweed, buttercup, and members of the bean families. The ratio assemblage at both lakes displays similar trends where spruce pollen is decreased relative to other taxa between 1930 and 1940 CE, and again between 1980 and 1990 CE (Figures 5 and 6).

Markagunt Plateau

Arboreal pollen on the Markagunt Plateau are composed of spruce (37%), fir (10%), pine (20%), and aspen (2–3%) (Figures 7 and 8). Shrubs at both lakes are composed mostly of rose (4–5%) and sagebrush (5–10%) while influx for both taxa are relatively higher at Morris Pond (Figure 8). Herbaceous taxa are dominated by grasses (10% at Morris Pond and 4% at Alpine Pond) and members of the sunflower family (≤5%) with average influx for herbs also greater at Morris Pond. Other herbaceous components are present at low values (1–2%; <100 grains/cm^3) including bell flower (Campanulaceae), pink (Caryophyllaceae), buttercup, and bean families. The ratio assemblage at both lakes displays similar trends where spruce pollen is dominant in the ratio until *c*. 1980 CE where it declines through the remainder of the records (Figures 7 and 8).

Discussion

Pollen

During a SB epidemic, mortality of the generally taller and longer-lived Engelmann spruce creates canopy gaps that increase

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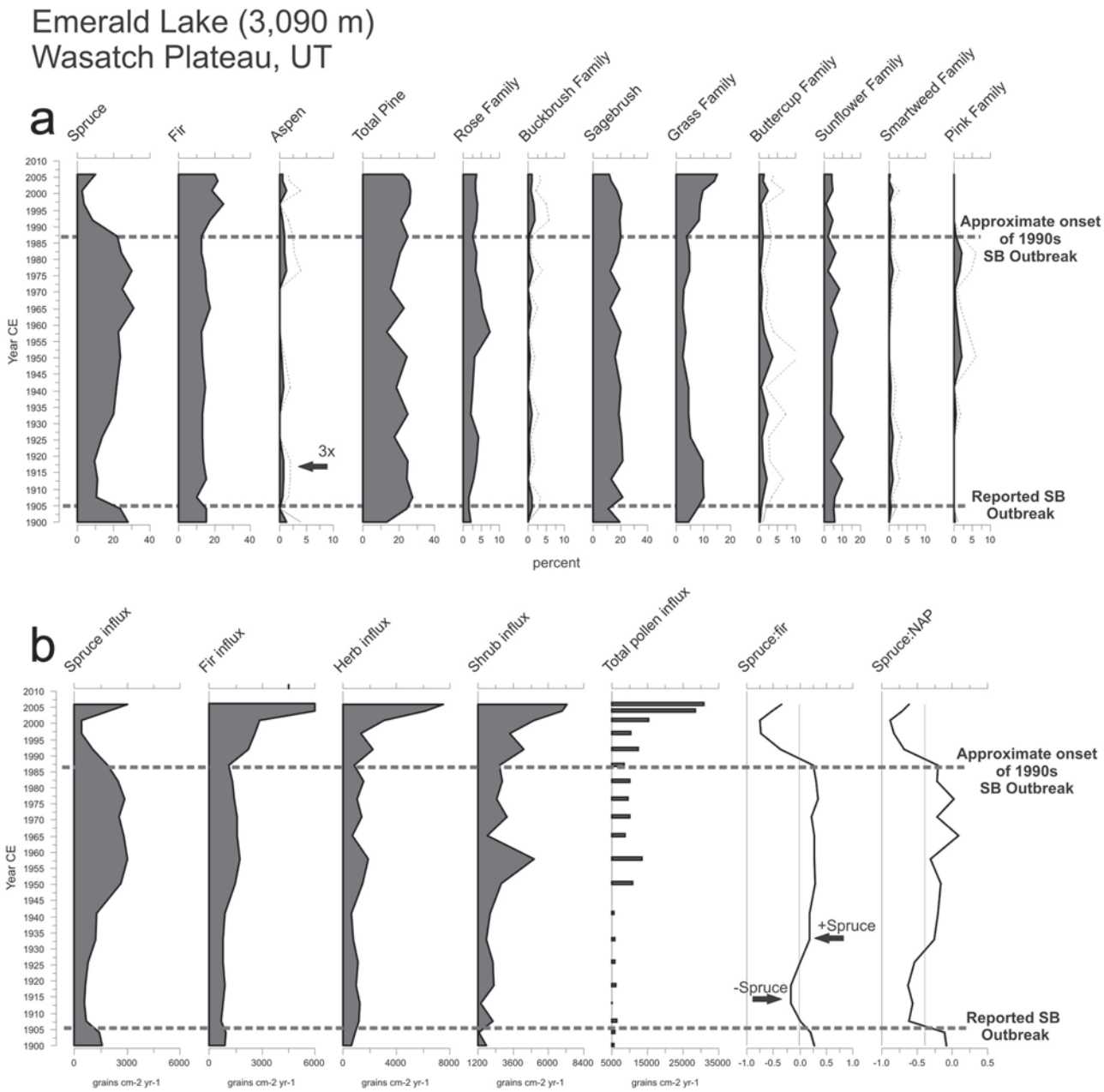

Figure 4. 20th century pollen percent (a) and pollen influx and ratio (b) plots for Emerald Lake, located on the Wasatch Plateau, UT. Dashed plot lines indicate 3× exaggeration. A severe spruce beetle outbreak impacted the subalpine forests surrounding Emerald Lake beginning in the late 1980s CE and an endemic outbreak occurred near Emerald Lake around 1905 CE. Pollen ratios were calculated $(a-b)/(a+b)$ where a represents spruce (host) and b represents fir and non-arboreal pollen (NAP; non-host). Higher ratio values indicate greater abundance of spruce pollen whereas lower values indicate less spruce pollen. Ratio thresholds are calculated as the 20th century ratio average (gray line).

availability of sunlight, nutrients, and growing space which invigorate understory arboreal and non-arboreal species (Figure 1, panel c). The resulting growth release of the forest understory (subalpine fir and small diameter spruce) has been observed in numerous stand surveys during and immediately after SB outbreaks (DeRose and Long, 2007; Dymerski et al., 2001; Holsten et al., 1995; Schmid and Frye, 1977). For example, a SB epidemic in Colorado modified the canopy from 90% Engelmann spruce and 10% subalpine fir to 20% and 80%, respectively (Schmid and Hinds, 1974). Ground surveys indicate similar changes in Utah on the Wasatch (Dymerski et al., 2001) and Markagunt plateaus (DeRose and Long, 2007). Dendroecological records suggest that elevated ring-width growth in non-host trees (subalpine fir) may persist for up to 40 years after a SB outbreak (Veblen et al., 1991, 1994). These distinct changes in vegetation composition and structure following a SB outbreak provide the theoretical framework for examining how these vegetation responses might be recorded in sedimentary pollen accumulations.

The six pollen records presented here reflect known ecological conditions contemporaneous with historic SB outbreaks. For example, decreasing spruce pollen following mortality is accompanied by concurrent increases in fir pollen (Figures 3–8). This feature is evident across all sites and pollen indices (both percentage and influx). Generally, herb and shrub pollen also increase during a SB outbreak, although examination of individual percentage and influx data (e.g. Figure 6) appears less compelling than a comparison of spruce pollen to fir and NAP (i.e. ratio). To provide context, ratios present in Figures 3–8 are plotted against their respective 20th century ratio average. Ratio trends are broadly consistent across sites, while ratios of spruce to fir appear to remain lower (i.e. less

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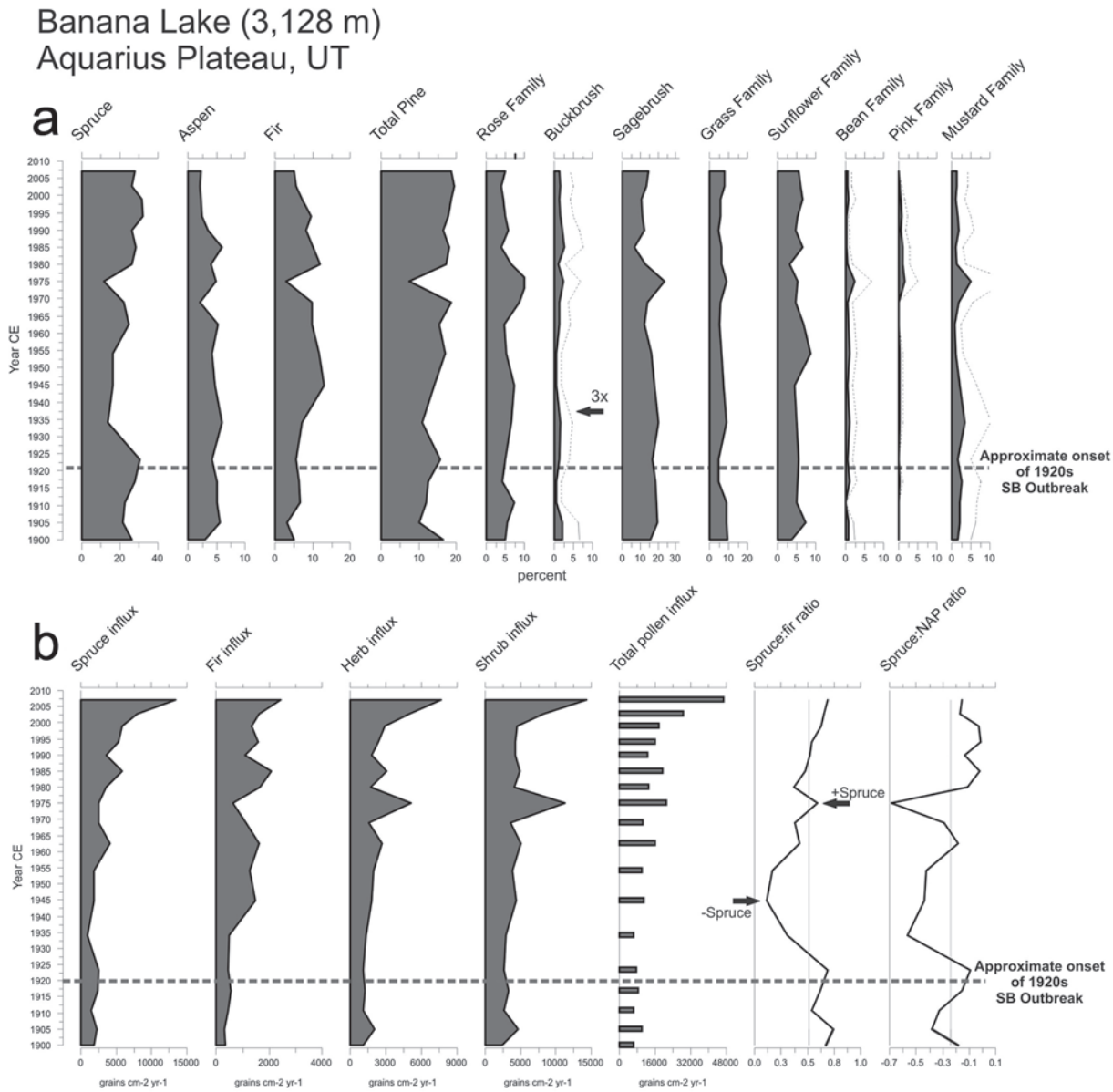

Figure 5. 20th century pollen percent (a) and pollen influx and ratio (b) plots for Banana Lake, located on the Aquarius Plateau, UT. Dashed plot lines indicate 3× exaggeration. A severe spruce beetle outbreak impacted the subalpine forests surrounding Banana Lake beginning in the late 1910s CE and persisted into the early 1940s CE. Pollen ratios were calculated $(a-b)/(a+b)$ where a represents spruce (host) and b represents fir and non-arboreal pollen (NAP; non-host). Higher ratio values indicate greater abundance of spruce pollen whereas lower values indicate less spruce pollen. Ratio thresholds are calculated as the 20th century ratio average (gray line).

abundance of spruce) several decades following an outbreak at Banana Lake (Figure 5). The robustness of the spruce:fir ratio signal is probably due to two factors: (1) the greater longevity of trees relative to shrubs and herbs and (2) canopy closure following the release of residual understory trees eventually outcompetes shrubs and herbs. Therefore, in the context of Holocene pollen records, examining host pollen to non-host tree(s) is of greater advantage than ratios to NAP because of the increased likelihood of detecting the signal in a practical core sampling strategy.

However, in the case of Purple Lake the reponse in the spruce:fir and spruce:NAP ratio lags the known outbreak. This could be due to error in the core chronology or that the outbreak did not reach Purple Lake until later than observed in other areas of the AqP. The pollen signature of the outbreak is more subtle at Purple Lake in general. This is probably because the vegetative community surrounding Purple Lake is composed primarily of Engelmann (host) and blue (not a preferred host) spruce which are palynologically indistinguishable from one another. There is only small subalpine fir component at this lake. Following the 1930s SB infestation, the advanced regeneration occurred mostly in Englemann spruce (Figure 1, panel c). Interestingly, a fire (1 ha) occurred in July of 1993 CE in the Purple Lake watershed (United States Forest Service, unpublished data, 2010) which registers conspicuously across both ratios. While the spruce pollen declines (Figure 6), post-fire colonization by herbaceous taxa is evident and more rapid than arboreal species. This is not surprising because arboreal species require more time to mature and produce pollen, which suggests that using a ratio of arboreal pollen to herbaceous pollen may be useful in detecting fire disturbance. However, the ecological change from this fire event appears comparable to the severe SB event that took place during the 1920s. This suggests that watersheds composed predominantly of arboreal pollen types that are not diagnostic among host/non-host are not ideal for assessing bark beetle outbreaks.

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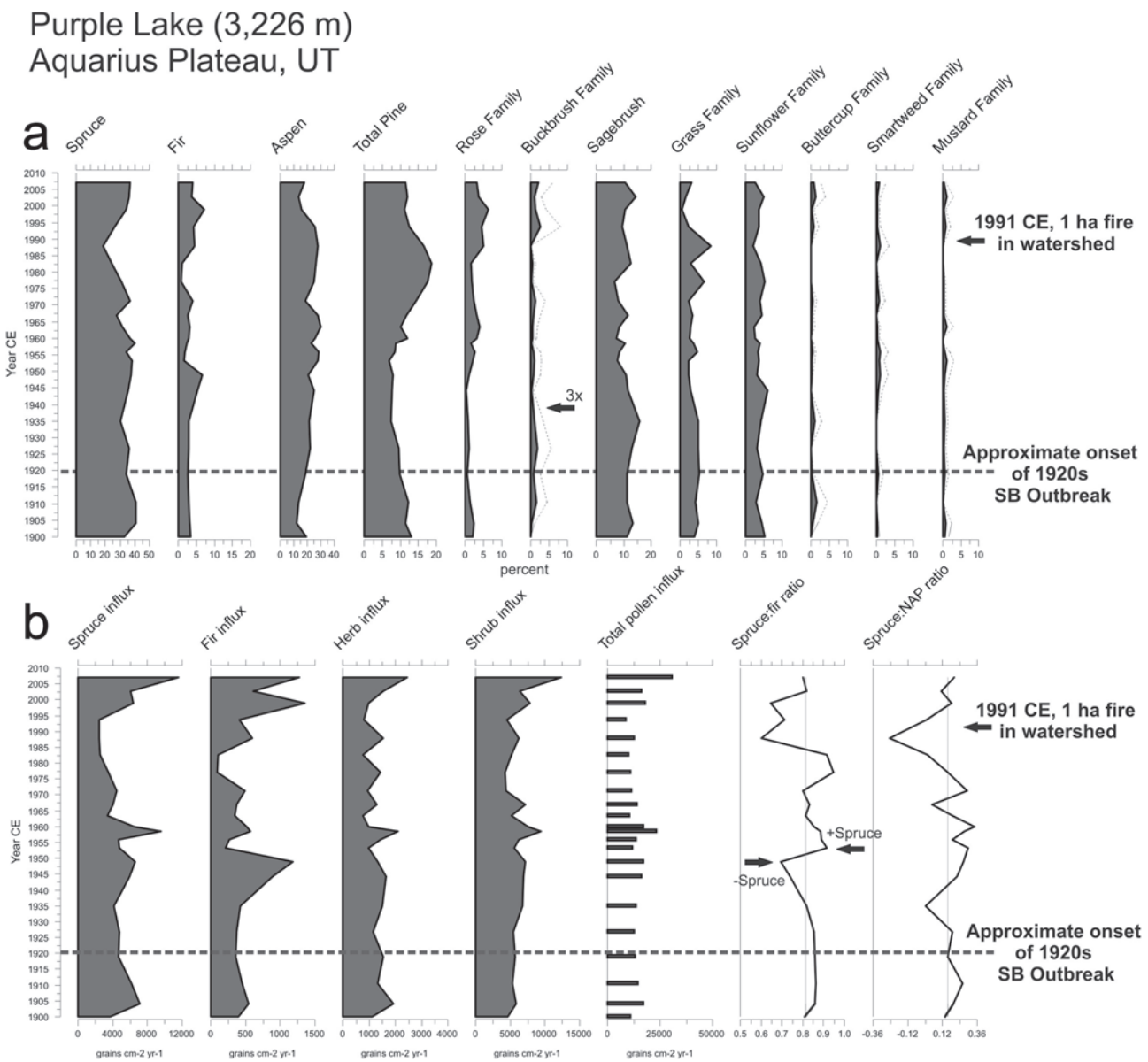

Figure 6. 20th century pollen percent (a) and pollen influx and ratio (b) plots for Purple Lake, located on the Aquarius Plateau, UT. Dashed plot lines indicate 3× exaggeration. A severe spruce beetle outbreak impacted the subalpine forests surrounding Purple Lake beginning in the late 1910s CE and persisted into the early 1940s CE. Pollen ratios were calculated $(a-b)/(a+b)$ where a represents spruce (host) and b represents fir and non-arboreal pollen (NAP; non-host). Higher ratio values indicate greater abundance of spruce pollen whereas lower values indicate less spruce pollen. Ratio thresholds are calculated as the 20th century ratio average (gray line).

Macrofossils

Schmid and Frye (1977) report that during an SB outbreak in July 1949 CE, accumulations of SB carcasses were observed in drifts for at least 1 km along the shore of Trappers Lake on the White River Plateau in western Colorado. Based on this report it is not surprising that Brunelle et al. (2008) recovered MPB remains from lake sediments coincident with historic bark beetle epidemic (MPB remains were also identified in sediments dating to the early Holocene). However, no SB remains were found in any of the sediment cores analyzed for this study. Morris et al. (2010) determined that lake water chemistry is probably an important factor in preserving the diagnostic features of the chitinous remains of bark beetles and clearly the taphonomic process of bark beetle carcasses, such as those presented in Brunelle et al. (2008), requires systematic evaluation.

For insect remains to be deposited in lake sediments, the adult beetle must come in contact with surface water, which is probably a rare occurrence because SB and other bark beetles spend the majority of their life in subcortical chambers of the host tree and emerge for flight only briefly (about a week) during their 1–2 yr lifespan (Holsten et al., 1999). In the Rocky Mountain-region SB emergence typically occurs in June when daily maximum temperatures reach ≈16°C (Dyer, 1969; Fettig et al., 2007). During June of 1949 CE, the summer when Schmid and Frye (1977) report on the extensive SB carcass drifts at Trappers Lake, the National Climate Data Center reports for Colorado Division 4 that June 1949 was the single wettest June during the 20th century (National Climate Data Center, 2010). This suggests that precipitation during peak SB emergence adversely affected beetle flight and contributed to the carcass drifts reported in Schmid and Frye (1977).

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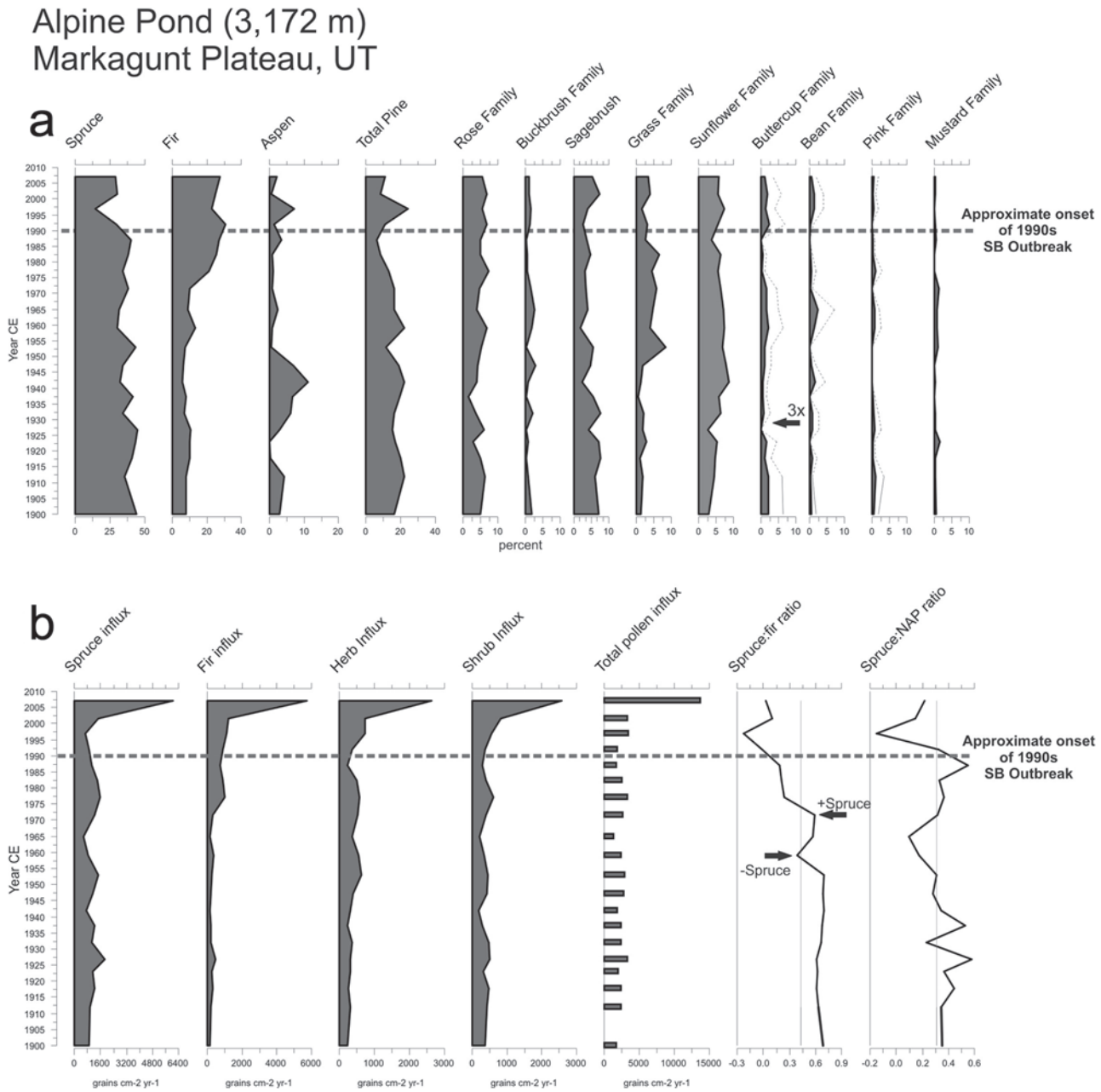

Figure 7. 20th century pollen percent (a) and pollen influx and ratio (b) plots for Alpine Pond, located on the Markagunt Plateau, UT. Dashed plot lines indicate 3× exaggeration. A severe spruce beetle outbreak impacted the subalpine forests surrounding Alpine Pond beginning in the early 1990s CE and persisted into the early 2000s CE. Pollen ratios were calculated $(a-b)/(a+b)$ where a represents spruce (host) and b represents fir and non-arboreal pollen (NAP; non-host). Higher ratio values indicate greater abundance of spruce pollen whereas lower values indicate less spruce pollen. Ratio thresholds are calculated as the 20th century ratio average (gray line).

Conclusions

While the results of this study represent a significant compilation of data and multiple high-resolution historical assessments, this study is not a rigorous statistical analysis. Even with every centimeter of the core analyzed for the 20th century there are not enough samples for the historic period to produce a large enough n-value for a robust statistical analysis. What is presented instead are qualitative pollen representations that include percentages, influx, and ratios reflecting the loss of host spruce and growth release of non-host taxa for all six lakes analyzed in this study. These results offer a practical method with which to assess other palynological records.

In the six cores we examined for this study, the spruce:fir and spruce:NAP ratios decrease conspicuously during known SB outbreaks which provides guidelines for detecting SB disturbance using pollen. Determining a single quantitative threshold on ratios is problematic for 20th century outbreaks because of the low sample size (n=14 to 20), despite an analysis being conducted every contiguous centimeter. Statistical approaches among multiple sites are also inherently problematic because of differences in forest composition, successional stage, and lake surface area (pollen catchment) which all influence pollen accumulation. However, the palynological signal of a SB epidemic is clear at each lake and provides a framework for identifying large magnitude outbreaks over the Holocene. The assessments will of course become more

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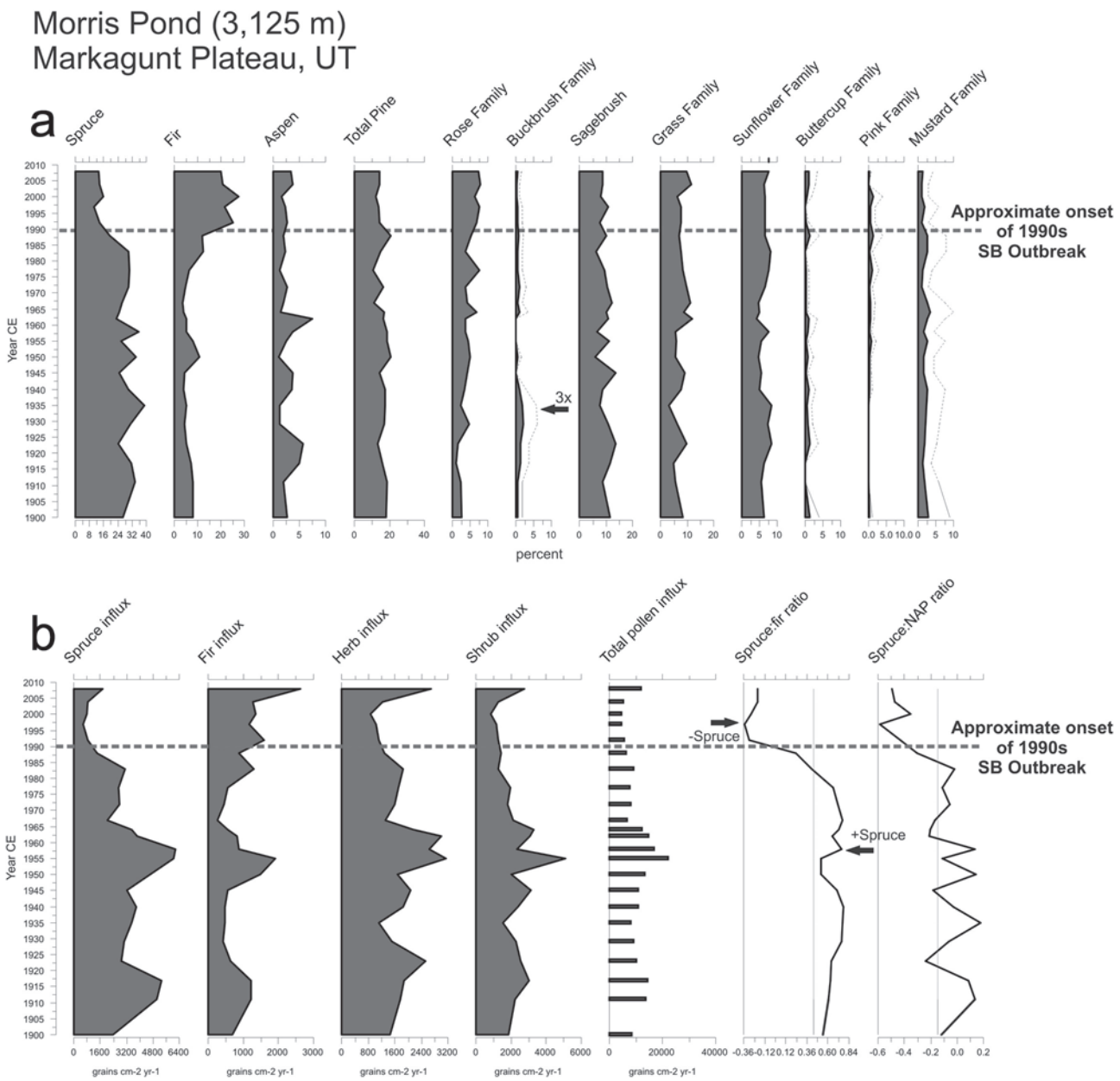

Figure 8. 20th century pollen percent (a) and pollen influx and ratio (b) plots for Morris Pond, located on the Markagunt Plateau, UT. Dashed plot lines indicate 3× exaggeration. A severe spruce beetle outbreak impacted the subalpine forests surrounding Morris Pond beginning in the early 1990s CE and persisted into the early 2000s CE. Pollen ratios were calculated $(a-b)/(a+b)$ where a represents spruce (host) and b represents fir and non-arboreal pollen (NAP; non-host). Higher ratio values indicate greater abundance of spruce pollen whereas lower values indicate less spruce pollen. Ratio thresholds are calculated as the 20th century ratio average (gray line).

robust with the addition of secondary and or supporting lines of evidence, such as beetle remains (Brunelle et al., 2008), geochemical markers, and paired studies with tree-rings. Overlapping high-resolution pollen analysis with tree ring studies may offer more temporally extensive data sets that would facilitate rigorous statistical application. Using host/non-host pollen ratios is effective at describing known ecological conditions, but without secondary indicators interpreting bark beetle activity using pollen alone provides a conservative estimate and likely only captures high magnitude events. Sediment compression (more time per centimeter), shifts in climate regimes and insolation dynamics, and no-analog vegetative communities (Williams and Jackson, 2007) are considerable challenges that could potentially be overcome by analyzing for a suite of pollen ratios, such as host versus non-host taxa (or group of taxon), in tandem with a supporting line of physical evidence.

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